

AGE STRUCTURE OF NEOTROPICAL MIGRANTS DURING FALL MIGRATION IN SOUTH DAKOTA: IS THE NORTHERN GREAT PLAINS REGION AN INLAND “COAST”?

KURT L. DEAN,^{1,2} HEATHER A. CARLISLE,^{1,3} AND DAVID L. SWANSON^{1,4}

ABSTRACT.—Proportions of juvenile birds in migrant populations at coastal stopover sites are often higher than proportions of juveniles at inland stopover sites, a phenomenon called the “coastal effect.” The northern Great Plains forms the western boundary of the migratory ranges for many Neotropical woodland migrants. Moreover, woodland habitat is scarce in this region, consisting primarily of natural riparian corridor woodlands (hereafter corridors) and planted woodlots and shelterbelts around farmsteads and agricultural fields (hereafter woodlots). Due to the scarcity of woodland habitat, one might expect that adults—by virtue of their experience and better-developed navigational abilities—would avoid the Great Plains during fall migration, thus producing age structures in migrant populations similar to those found at coastal sites. We tested this “inland coast” hypothesis for Neotropical migrants captured during fall migration at corridor and woodlot stopover sites in southeastern South Dakota. We classified migrants into three groups based on whether our South Dakota study sites were peripheral (western edge of migratory range within South Dakota), near-peripheral (western edge in, or just west of, Wyoming or Montana), or central (western edge well west of Montana and Wyoming) to their regular migratory ranges. We captured higher juvenile proportions of peripheral ($86.5 \pm 10.4\%$, 2 species) and near-peripheral ($85.6 \pm 4.5\%$, 7 species) migrants than central migrants ($79.6 \pm 7.2\%$, 5 species), but the difference was not significant ($P = 0.11$). The proportion of juveniles was inversely correlated with the distance of our study sites from the western edge of a given species’ migratory range ($r = 0.476$, $P = 0.085$). The proportion of juvenile Neotropical migrants at our study sites was near the upper end of proportions recorded for other inland sites in North America, but was slightly lower than those recorded at coastal sites. Our results are, therefore, only partially consistent with the inland coast hypothesis, suggesting that factors other than geographic location also shape age structures at our study sites. The mean proportion of juveniles (for species captured ≥ 13 times in both habitats; $n = 10$) was significantly greater ($P = 0.002$) in the woodlot ($89.1 \pm 7.0\%$) than in corridors ($73.8 \pm 12.5\%$). The differential age structure in the two habitats suggests that habitat characteristics may influence age structure of the migrant community, but mechanisms for such an influence are currently unknown. Received 5 August 2003, accepted 21 October 2004.

Variation in age structure among Neotropical migrants at stopover sites during migration may indicate age-related differences in the selection of migration routes (Clench 1969, Ralph 1981), timing of migration (Drury and Keith 1962, Hussell et al. 1967, Stewart et al. 1974, Hall 1981), or navigational abilities (Drury and Keith 1962, Ralph 1978). Ralph (1971, 1978) proposed that age-related differences in migratory orientation abilities and experience may lead to a higher-than-expected incidence of juvenile birds at coastal sites or at the peripheries of migratory routes, a so-called “coastal effect.” Most of the data

supporting these conclusions were derived by comparing age structures and densities at coastal stopover sites with similar data from interior sites (Drury and Keith 1962; Murray 1966; Ralph 1971, 1978, 1981). Subsequent research has confirmed the generally high proportion of juveniles at coastal stopover sites (Hall 1981, Stewart 1986, Taylor et al. 1994, Morris et al. 1996, Woodrey and Moore 1997). Ralph (1981) further argued that sites with higher percentages of juveniles and lower overall densities were principal criteria for defining the periphery of a species’ migration route. This argument implies that the causative factor for the high proportions of juveniles at coastal sites is that they are peripheral to the main migratory route for the species. The basis for this argument is the unproven assumption that following a main migratory route is an adaptive behavior, and that individuals straying from these routes suffer increased mortality, and thereby reduced fitness (Ralph 1981). The coastal effect could also

¹ Dept. of Biology, Univ. of South Dakota, Vermillion, SD 57069, USA.

² Current address: Dept. of Biology, Central Missouri State Univ., WCM 306, Warrensburg, MO 64093, USA.

³ Current address: PRBO Conservation Science, 4990 Shoreline Hwy. 1, Stinson Beach, CA 94970, USA.

⁴ Corresponding author; e-mail: dlswanso@usd.edu

result from young birds seeking out coastal habitats for a variety of reasons (e.g., better food resources, decreased competition with adults, navigational purposes). None of these alternatives has been adequately addressed and the causative factors underlying the coastal effect are not well understood. If, however, Ralph's (1981) assumption—that the periphery of a migratory route confers lower fitness—is valid, and juveniles occur in higher proportions at the periphery due to less effective navigation, then the proportion of juveniles at the periphery of a species' migratory route should be high relative to more-central sites, whether coastal or inland.

Age structures during fall migration have been documented for several inland sites (Ralph 1971, 1978, 1981; Stewart et al. 1974; Hall 1981; Rimmer and McFarland 2000), but none of these sites lies near the inland boundary of the migratory ranges for migrants typically associated with forested areas in eastern North America. Consequently, the age compositions of fall migrants at inland peripheries of routes are essentially unknown. The northern Great Plains lies on the western periphery of migratory routes used by a number of eastern migrants (American Ornithologists' Union 1998). Current landscapes of the eastern portion of the northern Great Plains consist mainly of agricultural habitats interspersed with pastures and grasslands. Woodland habitats in this region are scarce, composing only about 4% of land area in southeastern South Dakota. Historically, they consisted mainly of natural, deciduous riparian woodlands bordering streams and rivers (hereafter corridors), but they have since been supplemented with woodlots and shelterbelts surrounding farmsteads and agricultural fields (hereafter woodlots). Of the current woodland area in southeastern South Dakota, 60 and 40% is composed of woodlots and corridors, respectively (Castonguay 1982). If adult birds are capable of more refined orientation during migration than juveniles, then it might be expected that they would avoid the relatively inhospitable landscapes of the northern Great Plains, which would result in age structures skewed toward juveniles in this region. As a consequence, age structures of migratory populations in this area might resemble coastal age structures, at least for those species for which the northern

Great Plains are peripheral to the main migratory range. A corollary prediction of the coastal effect hypothesis is that the proportion of juveniles should be greater in migratory populations of peripheral species than central species.

We evaluated the age structure of Neotropical migrant passerines captured at corridor and woodlot study sites during fall migration in southeastern South Dakota to delineate age-related migratory patterns in the northern Great Plains. Our objectives were to determine (1) whether coastal-like proportions of juveniles occurred at these study sites, (2) whether the proportion of juveniles in migrating populations differed between peripheral and central species, and (3) whether proportions of juveniles differed between corridor and woodlot study sites—the two habitats that represent the major types available to woodland migrants seeking stopover sites in this area.

METHODS

Study sites.—We captured Neotropical migrants with mist nets (9 × 2.6 m, 30 mm mesh) at four corridor sites in Clay and Union counties in southeastern South Dakota during fall migration (15 August–6 October) from 1993 through 1995. Three of the study sites were located in riparian corridor habitats along the Missouri and Big Sioux rivers. The fourth study site was located on a north-south tributary of the Big Sioux River (Bule Creek), and included both upland and riparian deciduous habitats. Migrants were also captured with mist nets at a single farmstead woodlot study site (~3.5 ha) during fall migration (15 August–6 October) in 1996 and 1997. These study sites and their vegetation are described in detail in Dean (1999) and Swanson et al. (2003). Because we sampled in corridor and woodlot study sites in different years, between-year differences might confound comparisons of age structure between sites; however, Ralph (1981) showed that 2 years of intensive sampling produced juvenile percentages within 5% of long-term averages for 95% of all species. Because we sampled intensively for at least 2 years at each study site, our data should accurately reflect the long-term age structure of migrants at these sites. Moreover, early August to early October

TABLE 1. Percent juveniles and total captures (*n*) for Neotropical migrant species (≥ 15 overall captures) at corridor and woodlot stopover sites in southeastern South Dakota, 1993–1997.

	Corridor		Woodlot		Overall
	%	<i>n</i>	%	<i>n</i>	%
Central migrants					
“Traill’s” Flycatcher (<i>Empidonax traillii</i> and <i>E. alnorum</i>)	60.8	51	91.2	34	72.9
Swainson’s Thrush (<i>Catharus ustulatus</i>)	81.8	11	75.0	4	80.0
Orange-crowned Warbler (<i>Vermivora celata</i>)	69.5	141	75.0	196	72.7
Nashville Warbler (<i>Vermivora ruficapilla</i>)	83.8	74	92.5	199	90.1
Wilson’s Warbler (<i>Wilsonia pusilla</i>)	70.5	44	85.9	142	82.3
Near-peripheral migrants					
Least Flycatcher (<i>Empidonax minimus</i>)	50.0	16	89.1	55	80.3
Red-eyed Vireo (<i>Vireo olivaceus</i>)	83.7	43	100.0	13	87.5
Tennessee Warbler (<i>Vermivora peregrina</i>)	0.0	1	95.8	24	92.0
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	81.8	22	85.9	64	84.9
Black-and-White Warbler (<i>Mniotilta varia</i>)	70.0	10	90.9	11	81.0
Ovenbird (<i>Seiurus aurocapilla</i>)	87.5	16	91.7	24	90.0
Northern Waterthrush (<i>Seiurus noveboracensis</i>)	78.3	23	92.3	13	83.3
Peripheral migrants					
Mourning Warbler (<i>Oporornis philadelphia</i>)	69.0	29	83.9	62	79.1
Canada Warbler (<i>Wilsonia canadensis</i>)	100.0	5	90.9	11	93.8

encompasses the major migration period for both adults and juveniles of most species of Neotropical woodland migrants that move through southeastern South Dakota, except perhaps, for later-migrating individuals of late migrants, such as Orange-crowned (*Vermivora celata*) and Yellow-rumped warblers (*Dendroica coronata*; Tallman et al. 2002).

Capture techniques.—Mist nets were placed at specific locations within each study site during fall migration; the same net locations were used throughout the study (both within and between years) at both corridor and woodlot study sites. Weather permitting, mist-netting was conducted 7 days per week at corridor sites and at least 6 days per week at the woodlot site. We opened 5–7 nets at each corridor site and 7–10 nets in the woodlot site; net hours were recorded as one net open for 1 hr = 1 net-hr. We sampled corridors only in the morning (sunrise until approximately 11:00 CST), whereas we sampled the woodlot in mornings and often evenings (for 2–3 hr prior to sunset) as well (Dean 1999, Swanson et al. 2003). Mist-netting at corridor sites occurred on a 4-day rotation so that each site was visited every 4th day—except during fall 1995, when flooding prevented continuous access to the Big Sioux River site. During the period of flooding, we alternated between the

two Missouri River study sites and the Brule Creek site on alternate days. Nets were not opened on rainy or very windy days. Total net-hr were 2,050 for corridor sites and 5,107 for the woodlot site (Dean 1999, Swanson et al. 2003).

Age structure analysis.—All birds were aged (hatching year = HY, after hatching year = AHY) by skull ossification, which is a reliable aging technique through at least the month of September for most Neotropical migrant passerines (Pyle 1997). For analysis of the “inland coastal effect,” we classified migrants into three groups (peripheral, near-peripheral, and central) based on the degree to which our study sites were peripheral to their regular migratory range (Table 1). Division of migrant birds into these groups was based on the broad-scale migratory range maps in Sibley (2000) and the finer scale migration maps in Tallman et al. (2002). If the western border of the main migratory range fell within South Dakota, we classified species as peripheral migrants; if the western border of the main migratory range at the latitude of South Dakota fell in, or just west of Wyoming or Montana, we classified species as near-peripheral migrants; and, if the western border of the main migratory range fell well west of Montana and Wyoming, we classified species as central mi-

grants. Yellow-rumped Warbler was classified as a near-peripheral migrant because the Myrtle race (*D. c. coronata*) is a common fall migrant in eastern South Dakota, but is rare in western South Dakota and casual in western North America away from coastal wintering areas (Hunt and Flaspohler 1998, Tallman et al. 2002). We did not include migrants that regularly breed at our study sites because we could not reliably distinguish between local breeders and passage migrants from farther north. Grouping species into arbitrary associations (e.g., by migratory boundaries) introduces difficulties in analyses such as these because each species has range boundaries that are not identical to those of other species, and which may vary temporally. However, because we were interested in broad-scale patterns of age structure that should apply generally to migrants—depending on the relative degree to which our sites are peripheral to the migratory range—we contend that pooling species into these groups does provide an adequate test of the “inland coast” hypothesis.

Migratory group comparisons.—We analyzed differences in juvenile proportions among migratory groups by calculating the percentage of juveniles for individual species captured ≥ 15 times and then calculating means for each group. Percentage data were arcsine-transformed prior to calculating means and we used one-way ANOVA to compare group means. Because only two species of peripheral migrants met the criterion of ≥ 15 captures, the power of one-way ANOVA to detect differences among means was very low. Consequently, we also compared mean juvenile proportions of pooled peripheral and near-peripheral migrants (means for the two groups were essentially identical, see Results) with central migrants by *t*-test.

We also calculated Pearson's correlation coefficients to test for correlations between proportions of juveniles at our study sites and distance to the edge of the migratory range. To determine distance to migratory range edge, we measured the approximate distance (nearest 50 km) to the migratory border (from maps in Sibley 2000) for each species at the latitude of our study sites (43° N) with the Geodetic II World Distance Calculator program, ver. 1.0 (www.infoairports.com/freeservices/worlddistance.html). For the Myrtle race of the Yellow-rumped

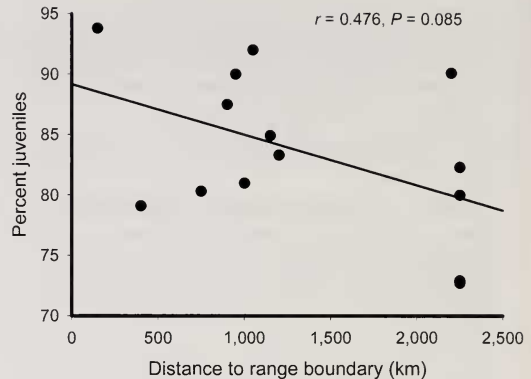


FIG. 1. Correlation between proportion of juveniles (species captured ≥ 15 times) for pooled corridor/woodlot sites and distances from our study sites to the approximate western boundaries of species' migratory ranges.

Warbler, whose migratory range Sibley (2000) depicts as extending west to the west coast of North America (where it is only a casual fall migrant *away from the coast*; Hunt and Flaspohler 1998), we arbitrarily selected the western border of Wyoming as the edge of its migratory range. Changing the western edge of the migratory range for this species by 500 km in either direction resulted in a maximum change of only 0.012 in the Pearson's correlation coefficient, so the exact position of the migratory boundary had little impact on our results.

Comparisons with other sites.—We used paired *t*-tests to compare mean proportions of juveniles for species that occurred at both our study sites (corridors and woodlot pooled) and other inland sites (see Fig. 1). We also calculated Pearson's correlation coefficients to test for correlations between latitude and proportions of juveniles at inland and coastal study sites. Latitudes for other study sites in North America, when not reported, were estimated (to the nearest 0.5° N) with the Geodetic II World Distance Calculator program.

Between-habitat comparisons.—For each migratory group, we used *t*-tests to compare mean percentages of juveniles in corridor sites versus the woodlot site [calculated for species captured ≥ 15 times in each habitat, but also including Red-eyed Vireo (*Vireo olivaceus*) and Northern Waterthrush (*Seiurus noveboracensis*), captured ≥ 15 times in corridors but only 13 times in the woodlot]. For between-habitat comparisons of juvenile proportions by

individual species (using only those species captured ≥ 15 times), we used a log-likelihood ratio for 2×2 contingency tables (G statistic, Zar 1996).

Additional statistics.—Median migration dates were established for species with ≥ 6 captures for each age class. Age-related synchrony of migration was compared using a median test 2×2 contingency table, which was analyzed by chi-square or Fisher's Exact tests (Zar 1996). Statistical significance for all tests was set at $P < 0.05$, except for paired t -tests of species that occurred at both our sites and other inland sites, and G -tests and median tests on individual species where multiple significance tests were required. For these tests, we used a sequential Bonferroni procedure (Rice 1989) to adjust α -levels and reduce the probability of type 1 errors, with $k = 7$ for paired t -tests, $k = 8$ for between-habitat comparisons for individual species, and $k = 6$ in both corridors and woodlots for median tests for individual species. Means are presented \pm SD.

RESULTS

Migration timing.—One factor influencing the variability of age structures at stopover sites may be age-related asynchrony in migratory timing. If sampling effort is not even over the entire migration period, or if peak migratory periods for specific age groups are undersampled, then calculations of age structures may be inaccurate (Kelly and Finch 2000). The age structures we report are not a reflection of asynchronous migration, as median migration dates of adults and juveniles did not differ ($P > 0.05$, all species).

Migratory group comparisons.—The proportions of juveniles (for species with ≥ 15 captures, Table 1) for peripheral migrants ($86.5 \pm 10.4\%$, $n = 2$ species), near-peripheral migrants ($85.6 \pm 4.5\%$, $n = 7$ species), and central migrants ($79.6 \pm 7.2\%$, $n = 5$ species) did not differ ($F_{2,11} = 1.474$, $P = 0.27$). The proportion of juveniles was higher for peripheral and near-peripheral migrants pooled ($85.8 \pm 5.3\%$) than for central migrants, but not significantly so ($t_{12} = 1.73$, $P = 0.11$). Twelve species of peripheral migrants were represented by fewer than 9 captures (48 individuals total): Yellow-bellied Flycatcher (*Empidonax flaviventris*), Eastern Phoebe

(*Sayornis phoebe*), Great Crested Flycatcher (*Myiarchus crinitus*), Blue-headed Vireo (*Vireo solitarius*), Philadelphia Vireo (*Vireo philadelphicus*), Golden-winged Warbler (*Vermivora chrysoptera*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Magnolia Warbler (*D. magnolia*), Black-throated Green Warbler (*D. virens*), Blackburnian Warbler (*D. fusca*), Bay-breasted Warbler (*D. castanea*), and Scarlet Tanager (*Piranga olivacea*). The pooled proportion of juveniles for these 12 species was 93.8%. The proportion of juveniles was inversely correlated (marginally; $r = 0.476$, $P = 0.085$) with the distances of our study sites from the edges of species' migratory ranges (Fig. 1).

Comparisons with other sites.—The proportion of juveniles captured in South Dakota fell within the range (corridor sites) or were near the upper end (woodlot site) of proportions recorded at other inland sites in North America (Fig. 2). Comparisons of shared migrant species revealed that South Dakota study sites had higher proportions of juveniles than all other inland sites, but in only one case was the difference significant (South Dakota versus Carlisle, PA; Table 2). Ralph (1981) considered individual species to exhibit coastal age ratios if the percentage of juvenile birds was $\geq 85\%$. For species with at least 13 captures in our study, coastal-like age ratios ($\geq 85\%$) were obtained for only 1 of 10 species in corridor sites, but for 9 of 11 species in the woodlot site (Table 1). The proportion of juveniles was not correlated with latitude for either inland ($r = 0.43$, $P = 0.25$) or coastal ($r = 0.07$, $P = 0.92$) sites (Fig. 3).

Between-habitat comparisons.—The proportion of juveniles was greater in the woodlot than in corridors for both peripheral/near-peripheral ($t_{10} = 2.82$, $P = 0.018$) and central ($t_6 = 2.55$, $P = 0.044$) migrants (pooled: 73.8 \pm 12.5% juveniles in corridors, 89.1 \pm 7.0% juveniles in woodlots; $t_{18} = 3.55$, $P = 0.002$; Fig. 4). Of the species captured ≥ 15 times in both corridors and the woodlot ($n = 8$ species), only "Traill's" Flycatcher (*Empidonax traillii* and *E. alnorum*; $G = 8.76$, $P = 0.004$) and Least Flycatcher (*E. minimus*; $G = 8.42$, $P = 0.004$) differed in age structure between corridors and the woodlot: for both species, there were greater percentages of juvenile birds in the woodlot than in corridors.

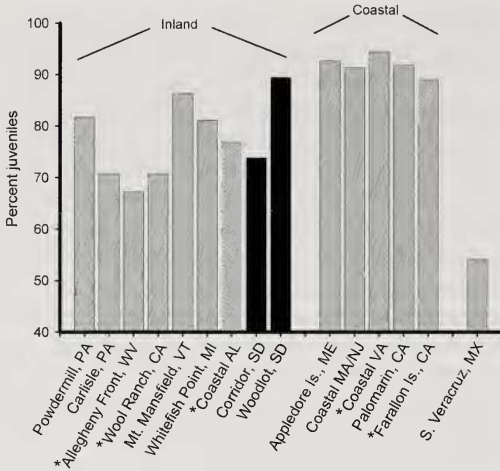


FIG. 2. Age structure of Neotropical woodland migrant populations at inland sites, coastal sites, and southern Veracruz, Mexico. Sites marked with asterisks do not represent the entire Neotropical migrant population, but studies at those sites included at least six commonly captured species of Neotropical migrants. Sites and data sources are as follows: Powdermill and Carlisle, PA, and coastal MA/NJ (Ralph 1981); Allegheny Front, WV (Hall 1981); Wool Ranch and Farallon Islands, CA (Stewart et al. 1974); Mt. Mansfield, VT (Rimmer and McFarland 2000); Whitefish Point, MI (R. Utych pers. comm.; data from fall migration seasons 1995–1997); coastal Alabama (Woodrey and Moore 1997); corridor and woodlot sites, SD (this study); Appledore Island, ME (Morris et al. 1996); coastal VA (Stewart 1986); Palomarin, CA (Taylor et al. 1994); and Veracruz, MX (Winker 1995). The coastal Alabama stopover site was included with the inland sites because it is far removed from the Atlantic coast and lies directly south of inland migration routes. The Veracruz site is unique due to the extreme narrowing of the continental landmass at that location, and is presented separately from inland and coastal sites.

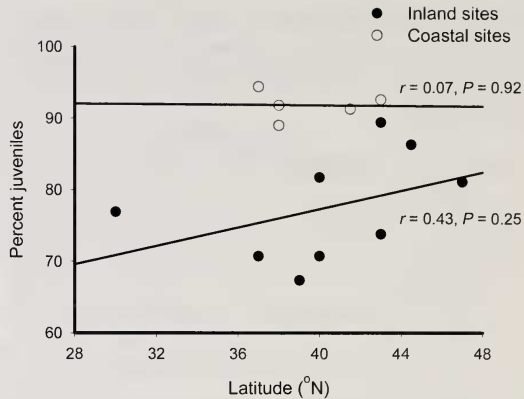


FIG. 3. Correlation between latitude and proportion of juveniles for nine inland and five coastal stopover sites in North America. There was no relationship between latitude and proportions of juveniles at either inland or coastal sites. Sources of data are the same as those listed for Figure 1.

DISCUSSION

Migratory group comparisons.—The proportions of juveniles among peripheral and near-peripheral migrants were slightly greater than they were for central migrants. The proportion of juveniles was inversely related to the distance of our sites from the boundaries of their migratory ranges ($P = 0.085$). Capture rates (this study) and abundance estimates from point counts (Dean 1999, Swanson et al. 2003) of peripheral and near-peripheral species also were typically lower than those for central migrant species, which is one of the criteria proposed by Ralph (1981) for delineating the periphery of a species’ migratory range. The pooled proportion of juveniles for

TABLE 2. Comparisons of mean proportions of juveniles (% HY \pm SD) common to South Dakota (pooled corridor and woodlot data) and seven other inland sites to the east of South Dakota. Comparisons were limited to Neotropical migrant species with ≥ 15 captures/site.

Site ^a	n ^b	% HY	South Dakota % HY	t	P
Powdermill, PA	11	75.1 \pm 13.8	84.6 \pm 4.6	2.26	0.048
Carlisle, PA	10	69.3 \pm 13.3	84.6 \pm 4.9	3.56	0.006 ^c
Allegheny Front, WV	3	70.1 \pm 5.1	88.1 \pm 5.1	9.51	0.011
Mt. Mansfield, VT	7	84.9 \pm 15.3	88.3 \pm 4.7	0.02	0.99
Whitefish Point, MI	13	81.9 \pm 14.4	84.4 \pm 6.0	0.45	0.66
Coastal AL	2	79.1 \pm 11.2	83.8 \pm 5.3	1.16	0.45
Southern Veracruz, MX	3	61.5 \pm 19.5	86.6 \pm 3.9	2.17	0.16

^a For sources of data, see Fig. 1.

^b Number of species occurring at both South Dakota sites and other sites.

^c Significant after sequential Bonferroni adjustment.

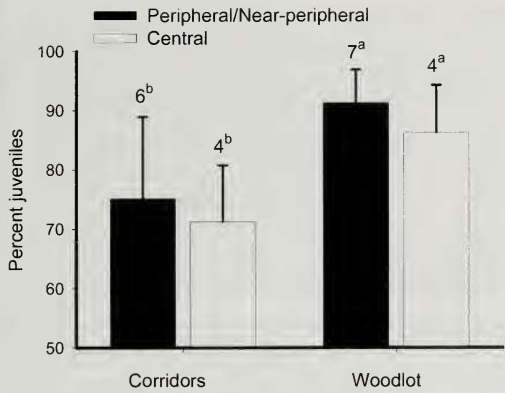


FIG. 4. Proportions of juveniles at corridor and woodlot sites, by two migratory groups, calculated using only species captured ≥ 15 times in both habitats (but also including Red-eyed Vireo and Northern Waterthrush, both of which were captured only 13 times in the woodlot). Sample sizes (number of species) are shown above bars. Bars with different letters (a, b) indicate significant differences ($P < 0.05$).

12 rarely captured species of peripheral migrants was 93.8%, similar to proportions of juveniles at coastal locations. Taken together, these data provide modest support for the inland coastal effect hypothesis.

Comparisons with other sites.—The proportions of juveniles at our study sites, especially at the woodlot, were at the upper end of proportions recorded at other inland sites in North America—also consistent with the inland coast hypothesis. Juvenile proportions for Neotropical migrant populations range from 91.3 to 94.4% HY birds at sites on both the east and west coasts of North America and from 67.3 to 86.3% HY birds at other inland sites (Fig. 2). However, relatively few species in our study had $\geq 90\%$ HY birds—a proportion commonly found at coastal sites. Our data, then, are not wholly consistent with our hypothesis of an inland coastal effect during fall migration whereby adults avoid the northern Great Plains. This suggests that geographic position relative to the main migratory range is not the only factor shaping age structure at inland stopover sites. Less extreme avoidance of the northern Great Plains than of coastal sites by adult birds makes some sense in terms of selection pressures on migrants. Although the northern Great Plains offer little favorable stopover habitat for woodland migrants, the fitness consequences of straying

over this region are not as overtly negative as those of straying over the open ocean.

The proportions of juvenile birds at several inland sites—including those in our study—were greater than the predicted 50–80% of fall populations based on clutch sizes and survival (Ralph 1981). While age structures at inland sites are not as heavily skewed toward juveniles as those at many coastal sites, in several cases inland and coastal sites showed only relatively minor differences. Potential explanations for the higher-than-expected incidence of juveniles at inland sites may include some or all of the following: high breeding productivity (e.g., double-brooding) of migrants (e.g., Holmes et al. 1992), high adult or low juvenile mortality, or lack of age-structure data from a sufficient number of inland sites to provide an accurate overall picture of geographic variation in age structure of eastern migrants. Further study is needed to distinguish between these possibilities.

Variation in age structure among sites might also be explained by differential mortality among age-classes. Annual mortality is highest for migrant birds during migration, and may account for up to 85% of annual mortality in some species (Sillert and Holmes 2002). Juveniles are thought to suffer heavy mortality rates during their first migration, especially when migrating over geographic barriers (Ralph 1978, Gauthreaux 1982, Goss-Custard et al. 1982, Moore et al. 1995). If juvenile mortality is higher than adult mortality during fall migration, then age structure should be more skewed toward adults with increasing distance along the migratory route. However, age structure was not significantly correlated with latitude for either coastal or inland sites in North America, suggesting little differential mortality among age classes.

Another possible method for indirectly assessing juvenile mortality during fall migration is to compare juvenile proportions for species at our study sites with those at stopover sites farther to the south, and therefore farther along the migratory route. Ceilometry data suggest that fall migrants in southeastern South Dakota adopt southeasterly headings (Dean 1999), which, if held constant, would lead them to coastal sites in southern Alabama or Mississippi, and then over or around the Gulf of Mexico. Juvenile proportions were

only slightly higher in southeastern South Dakota than in coastal Alabama (Woodrey and Moore 1997; Fig. 2). Moreover, for the two migrant species that occurred at both our study sites and the coastal Alabama study site, juvenile proportions were 87.5 and 87.0% (Red-eyed Vireo) and 80.0 and 71.9% (Swainson's Thrush, *Catharus ustulatus*) at South Dakota and Alabama sites, respectively. However, the proportion of juveniles was greater at our study sites than at the Isthmus of Tehuantepec in southern Mexico (Winker 1995). These data are consistent with similar mortality of adults and juveniles en route from South Dakota to Alabama, but higher juvenile mortality later in migration. Alternatively, this pattern might be explained by the unlikely possibility that fewer adults than juveniles make trans-Gulf flights (thereby bypassing the Isthmus of Tehuantepec), or by en route recruitment of juveniles along the migratory route. In any event, these data do not provide strong evidence for a high rate of juvenile mortality contributing to the difference in juvenile proportions among inland stopover sites.

Between-habitat comparisons.—Juvenile proportions were generally greater in the woodlot site than in corridor sites. Such a pattern could potentially arise from differences in habitat quality between corridors and woodlots. Vegetational structure and diversity differ among the two habitats: woodlots are generally small, isolated from each other, and exhibit low plant diversity; corridors are generally much larger, more contiguous, and have higher diversity (Dean 1999, Swanson et al. 2003). Because of these differences, corridors might be expected to provide better stopover habitat than woodlots. If corridors are better habitat for migrants than woodlots, then the previous experience and more refined navigational abilities of adult birds (Ralph 1981) would lead us to expect higher densities of adults than juveniles at corridor sites. This tendency could strengthen if adults competitively displace juveniles from corridor sites. If adults preferentially occupy higher-quality stopover sites, then juveniles might occur in greater proportions at lower-quality sites throughout the migratory range. Such a relationship could help explain the coastal effect (if coastal sites are generally inferior to inland

sites) and the relatively wide variation in proportions of juveniles at inland sites (Fig. 2).

Competition for food among migrants can occur at stopover sites and may be more intense where migrant densities are greater (Moore and Yong 1991, Kelly et al. 2002). The relatively small total area of corridor habitats in southeastern South Dakota might concentrate migrants at these sites, thereby increasing competition. However, densities of migrants were roughly similar at corridor and woodlot sites (Swanson et al. 2003). In addition, migrants were generally able to gain mass during stopover at the woodlot (Carlisle 1998, Swanson et al. 2003); thus, woodlots appear to serve as suitable stopover habitat. Inasmuch as relative stopover habitat quality at these sites has not been assessed directly, the contribution of habitat quality to differences in age structure is unknown. Moreover, the absence of marked age-related differences in rates of mass gain (Morris and Glasgow 2001, Jones et al. 2002) suggests that age-related competition may not be a major factor influencing age structures at stopover sites under most circumstances. Thus, the mechanisms responsible for differences in age-structure of migrants between corridors and woodlots in our study are unknown.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the assistance of the following individuals: J. S. Martin, D. P. Weinacht, E. T. Liknes, M. Trammel, and all of the undergraduate field assistants who toiled thanklessly for credit. We thank E. T. Liknes, J. D. Carlisle, M. S. Woodrey, C. J. Ralph, and three anonymous reviewers for helpful comments on previous versions of this manuscript. This project was funded in part by grants from the U.S. Fish and Wildlife Service Region 6 Nongame Migratory Bird Program and South Dakota Wildlife Diversity Program to DLS.

LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1998. Check-list of North American birds, 7th ed. American Ornithologists' Union, Washington, D.C.
- CARLISLE, H. A. 1998. Abundance, diversity, and energetic condition of Neotropical woodland migrants during stopover in a geographically isolated farmstead woodlot in southeastern South Dakota. M.A. thesis, University of South Dakota, Vermillion.
- CASTONGUAY, T. L. 1982. Forest area in eastern South Dakota, 1980. Research Note NC-291. U.S. Forest

- Service, North Central Forest Experiment Station, St. Paul, Minnesota.
- CLENCH, M. H. 1969. Additional observations on the fall migration of adult and immature Least Flycatchers. *Bird-Banding* 40:238–252.
- DEAN, K. L. 1999. Stopover ecology of Neotropical migrant songbirds in riparian corridors in the northern Great Plains. Ph.D. dissertation, University of South Dakota, Vermillion.
- DRURY, W. H. AND J. A. KEITH. 1962. Radar studies of songbird migration in coastal New England. *Ibis* 104:449–489.
- GAUTHREUX, S. A., JR. 1982. Age-dependent orientation in migratory birds. Pages 68–74 in *Avian navigation* (F. Papi and H. Wallraff, Eds.). Academic Press, New York.
- GOSS-CUSTARD, J. D., S. E. A. LE V. DIT DURELL, H. P. SITTERS, AND R. SWINFIN. 1982. Age structure and survival of a wintering population of oystercatchers. *Bird Study* 29:83–98.
- HALL, G. A. 1981. Fall migration patterns of wood warblers in the southern Appalachians. *Journal of Field Ornithology* 52:43–49.
- HOLMES, R. T., T. W. SHERRY, P. P. MARRA, AND K. PETIT. 1992. Multiple brooding and productivity of a Neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. *Auk* 109:321–333.
- HUNT, P. D. AND D. J. FLASPOHLER. 1998. Yellow-rumped Warbler (*Dendroica coronata*). *The Birds of North America*, no. 376.
- HUSSELL, D. J. T., T. DAVIS, AND R. D. MONTGOMERIE. 1967. Differential fall migration of adult and immature Least Flycatchers. *Bird-Banding* 38:61–66.
- JONES, J., C. M. FRANCIS, M. DREW, S. FULLER, AND M. W. S. NG. 2002. Age-related differences in body mass and rates of mass gain of passerines during autumn migratory stopover. *Condor* 104:49–58.
- KELLY, J. F., L. S. DELAY, AND D. M. FINCH. 2002. Density-dependent mass gain by Wilson's Warblers during stopover. *Auk* 119:210–213.
- KELLY, J. F. AND D. M. FINCH. 2000. Effects of sampling design on age ratios of migrants captured at stopover sites. *Condor* 102:699–702.
- MOORE, F. R., S. A. GAUTHREUX, JR., P. KERLINGER, AND T. R. SIMONS. 1995. Habitat requirements during migration: important link in conservation. Pages 121–144 in *Ecology and management of Neotropical migratory birds* (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.
- MOORE, F. R. AND W. YONG. 1991. Evidence of food-based competition among passerine migrants during stopover. *Behavioral Ecology and Sociobiology* 28:85–90.
- MORRIS, S. R. AND J. L. GLASGOW. 2001. Comparison of spring and fall migration of American Redstarts on Appledore Island, Maine. *Wilson Bulletin* 113:202–210.
- MORRIS, S. R., D. W. HOLMES, AND M. E. RICHMOND. 1996. A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. *Condor* 98:395–409.
- MURRAY, B. G. 1966. Migration of age and sex classes of passerines on the Atlantic coast in autumn. *Auk* 83:352–360.
- PYLE, P. 1997. *Identification guide to North American birds, part I*. Slate Creek Press, Bolinas, California.
- RALPH, C. J. 1971. An age differential of migrants in coastal California. *Condor* 73:243–246.
- RALPH, C. J. 1978. The disorientation and possible fate of young passerine coastal migrants. *Bird-Banding* 49:237–247.
- RALPH, C. J. 1981. Age ratios and their possible use in determining autumn routes of passerine migrants. *Wilson Bulletin* 93:164–188.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- RIMMER, C. C. AND K. P. MCFARLAND. 2000. Migrant stopover and postfledging dispersal at a montane forest site in Vermont. *Wilson Bulletin* 112:124–136.
- SIBLEY, D. A. 2000. *The Sibley guide to birds*. Alfred A. Knopf, New York.
- SILLETT, T. S. AND R. T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- STEWART, P. A. 1986. Fall migration of twelve species of wood warblers through coastal Virginia. *North American Bird Bander* 11:83–88.
- STEWART, R. M., L. R. MEWALDT, AND S. KAISER. 1974. Age ratios of coastal and inland fall migrant passerines in central California. *Bird-Banding* 45:46–57.
- SWANSON, D. L., H. A. CARLISLE, AND E. T. LIKNES. 2003. Abundance and richness of Neotropical migrants during stopover at farmstead woodlots and associated habitats in southeastern South Dakota. *American Midland Naturalist* 149:176–191.
- TALLMAN, D. T., D. L. SWANSON, AND J. S. PALMER. 2002. *Birds of South Dakota*, 3rd ed. South Dakota Ornithologists' Union, Aberdeen, South Dakota.
- TAYLOR, D. M., D. F. DESANTE, G. R. GEUPEL, AND K. HOUGHTON. 1994. Autumn populations of landbirds along central coastal California 1976–1986. *Journal of Field Ornithology* 65:169–185.
- WINKER, K. 1995. Autumn stopover on the Isthmus of Tehuantepec by woodland Nearctic-Neotropic migrants. *Auk* 112:690–700.
- WOODREY, M. S. AND F. R. MOORE. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* 114:695–707.
- ZAR, J. H. 1996. *Biostatistical analysis*, 3rd ed. Prentice Hall, Englewood Cliffs, New Jersey.